Entomol. exp. appl. 48: 293–300, 1988

Response of the egg parasitoid *Trichogramma pretiosum* to the sex pheromone of its host *Heliothis zea*

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Accepted: August 29, 1988

Key words: Lepidoptera, Noctuidae, *Heliothis zea*, Hymenoptera, Trichogrammatidae, *Trichogramma pretiosum*, egg parasitoid, sex pheromone, kairomone, host-community location, olfactometer

Abstract

This paper presents results of olfactometer experiments with the egg parasitoid *Trichogramma pretiosum* Riley (Hymenoptera: Trichogrammatidae) and its host the corn earworm moth, *Heliothis zea* (Boddie) (Lepidoptera: Noctuidae). The sex pheromone of the host significantly reduced the total number of border crossings between odour fields in the olfactometer. Also, female parasitoids made significantly more visits to the calling moth odour field than to the opposite control field in the olfactometer. Further, the wasps spent significantly more time in the olfactometer field containing the sex pheromone released by calling virgin moths, than in control fields. If non-calling virgin moths were used as odour source, the response was reversed and wasps were repelled by the odour of the moths, and the numbers of visits were evenly distributed over the four flow fields. These results are discussed in the context of foraging ecology of egg parasitoids.

Introduction

Parasitoid wasps of the genus *Trichogramma* employ a vast array of chemical cues in the search and successful attack of host eggs. Considerable knowledge has accumulated about the short range kairomones involved in host location and host recognition. Moth scales contain a contact kairomone that stimulates searching behaviour in *Trichogramma* spp. (Lewis *et al.*, 1972; Smits, 1982; Noldus & van Lenteren, 1985b; Zaborski *et al.*, 1987). Host accessory gland secretions, present on and around lepidopteran eggs, cause arrestment and induce host recognition by the parasitoids (Noldus & van Lenteren, 1985b; Nordlund *et al.*, 1987; Pak and de Jong, 1987). Less is known about long distance search for hosts. Plant odours seem to play a role in host-habitat location by *Trichogramma* (Altieri *et al.*, 1981, 1982; Nordlund *et al.*, 1985). The present study deals with the means by which *Trichogramma* detect host communities (here defined as more or less spatially distinct host infestations) within a habitat. Recent research evidence indicates that the sex pheromone of the host may play a significant role in this respect. Lewis *et al.* (1982) found that eggs of the cotton bollworm, *Heliothis zea* (Boddie) (Noctuidae), were more heavily parasitized by naturally occurring *Trichogramma* spp. in cotton plots treated with synthetic sex pheromone of *H. zea* than in control plots. This finding aroused our interest about the behavioural mechanism underlying the observed effect. Increased parasitization in treated plots could

be due to attraction of parasitoids from a distance, arrestment and enhanced searching activity of local wasps, or both. Noldus & van Lenteren (1985a) studied this problem in a comparable host-parasitoid system: the cabbage armyworm, *Mamestra brassicae* and *T. evanescens*. In olfactometer experiments *T. evanescens* responded positively to the odour of calling virgin *M. brassicae* females, and not to that of non-calling mated females nor to that of male moths. Besides that, *T. evanescens* made significantly more visits to the calling moth odour field than to the opposite control field (Noldus, unpubl.). Here we present the results of olfactometer experiments designed to determine whether *T. pretiosum* Riley shows a similar response to its host *H. zea*.

Materials and methods

Parasitoids. The *T. pretiosum* wasps used in these experiments were from a laboratory culture originally obtained from Hermosilla, Mexico. The same stock was used by Lewis *et al.* (1982). The parasitoids were reared, following the procedure of Lewis & Redlinger (1969), on *H. zea* eggs at ca. 26 °C and 70% r.h., under a L14:D10 photoperiod (lights on at 06.00 h). For the experiments we used female wasps on the second day after emergence.

Prior to a test, female parasitoids were given an oviposition experience with *H. zea* eggs, according to the following procedure. Individual wasps were exposed for 30–60 min to 3–5 *H. zea* eggs that had been glued on a 5 × 25 mm strip of cardboard with rubber cement, in a 1 × 5 cm glass vial. The *H. zea* eggs had been obtained from a laboratory culture and had been washed with sodium hypochlorite as described by Burton (1969), irradiated with 25 krad (^{60}Co source) when 8–36 h old, and stored at ca. 10 °C for no longer than 24 h. The parasites were observed to insure that they parasitized at least one egg. The females were then isolated in empty glass vials and stored at 26 ± 1 °C for ca. 30 min prior to their use in experiments.

Hosts. H. zea moths were reared according to the procedure of Burton (1969). Pupae were sexed and separated, and allowed to emerge under reversed photoperiod (L14:D10, lights on at 19.00 h) to facilitate experiments during daytime. Under these conditions, onset of the scotophase for the moths coincided with the start of the 3rd hour of the photophase for the parasitoids. Adults were maintained on 10% sugar water at ca. 25 °C and 70% r.h. Virgin female moths were used between the 2nd and 8th hour of the scotophase, on the 2nd or 3rd night after emergence, when frequency of calling and pheromone release are highest (Pope *et al.*, 1984; Raina *et al.*, 1986). Male moths were used during the 2nd–4th scotophase.

Experimental set-up and procedure. Although the sex pheromone of *H. zea* has been chemically identified (Klun *et al.*, 1980) we used calling virgin moths as odour source, as we preferred to work with an odour blend as natural as possible, in order not to exclude any components that might be of relevance to the parasitoids. However, as the calling behaviour of *H. zea* consists of irregular bouts of extrusion of the abdominal tip (Agee, 1969), in contrast to female *Mamestra brassicae* moths, which often call for two hours or more, during one or two bouts (Subchev, 1980, 1983; Tóth, 1982; Attygalle *et al.*, 1987), it is difficult to obtain long periods of continuous calling in a laboratory set-up. Therefore, we constructed an experimental set-up, based on the one used by Noldus & van Lenteren (1985a), that allowed simultaneous observation of the activities of the wasp and monitoring of the behaviour of the moths (Fig. 1). The basic set-up consisted of a four-armed airflow olfactometer, modified after Vet *et al.* (1983). The olfactometer as described by Vet *et al.* is made of Plexiglas® , which has a low resistance to strong organic solvents and high temperatures, which makes thorough cleaning and removal of pheromone traces impossible. Instead of that, the central exposure chamber in our set-up was made of a piece of white acetal (Delrin®), milled to form the bottom and side walls of the chamber to which all connections were made, and a glass cover plate that could be screwed onto the bottompiece with four acetal bolts. The upper surface of the bottompiece was polished so smoothly that no measures were necessary to prevent air leaks between bottompiece and cover. Further, no glass containers were used between the odour

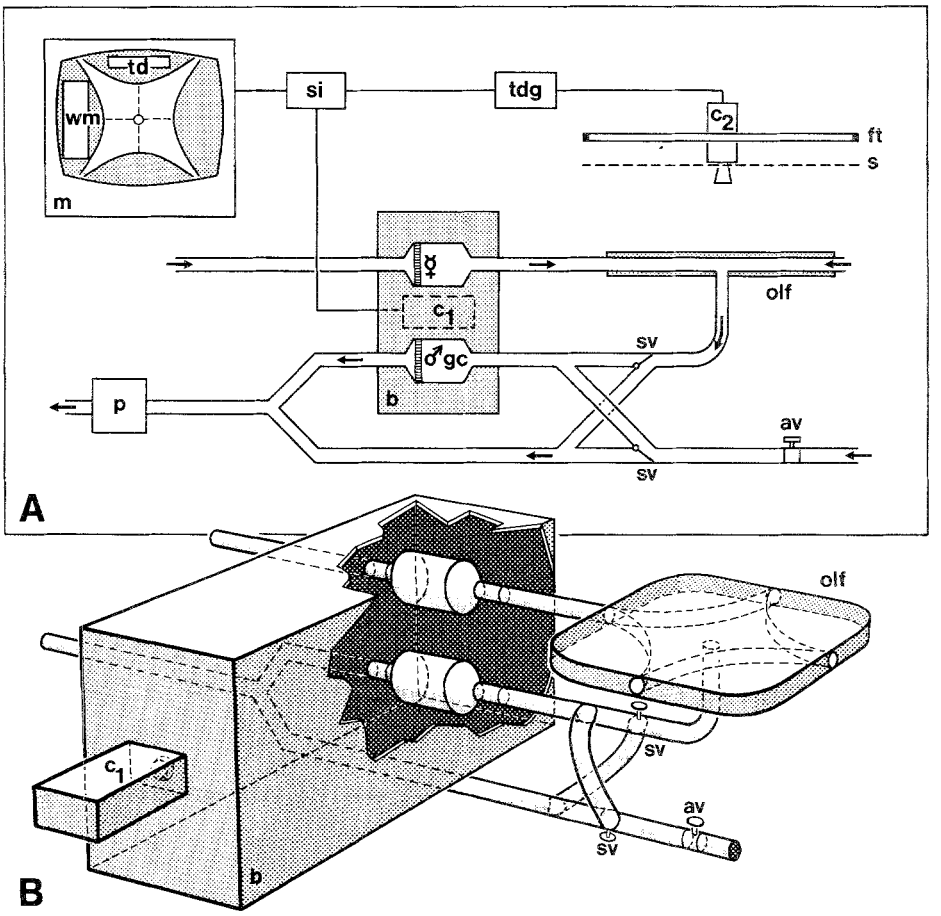

Fig. 1. A. Schematic representation of the olfactometer set-up and peripheral equipment. B. Detail of part of the set-up. *av*: adjustable valve; *b*: dark box; *c1*: camera 1; *c2*: camera 2; *ft*: fluorescent tube; *gc*: glass chamber with moths; *m*: video monitor; *olf*: olfactometer; *p*: membrane pump; *s*: diffusing screen; *si*: video splitter/inserter; *sv*: switching valve; *td*: time/date on monitor; *tdg*: time/date generator; *wm*: window showing moths. Arrows indicate the direction of the air flow.

sources and the exposure chamber of the olfactometer, to keep the distance between odour source and exposure chamber as small as possible.

In experiment 1, three of five virgin moths, used as odour source, were placed in a glass cylinder. This cylinder was constructed from a modified ground ball and socket joint held together by a metal clamp, 90 mm long × 25 mm ∅, with a fritted glass filter (max. pore diameter 175 μ) – for improved uniformity of the air flow inside the cylinder – on the upwind end, and was connected to one arm of the olfactometer. A second glass cylinder (with a fritted filter on the downwind end) containing 3–5 male moths was attached to the exhaust air stream, and their behaviour was used as a check for the actual presence of sex pheromone in the air stream. In order to prevent habituation of the males to the pheromone, air to this cylinder was controlled by an arrangement of switching valves that provided a selection of either clean air or olfactometer exhaust air to pass over the males. Most of the time, clean air was passed over them. The airstream flowing through the olfactometer was directed over the males at ca. 2 min intervals by simultaneously turning the two switching valves. The switching did not alter the speed of the air flow over either the females or the males (effectuated by an adjustable valve) in order to avoid disturbance of their behaviour. The cylinders holding both male and female moths were contained in a single light-controlled box, measuring 39 × 18 × 27 cm.

The activity of the moths was monitored, under

the light of a 4 watt red lamp, with the aid of a video camera (RCA TC 2000, 8 mm/1.4 lens, camera 1). The light intensity near the cylinders holding the moths was 6.8 lux. The olfactometer was illuminated by two fluorescent tubes, through a frosted glass plate to diffuse the light uniformly. The behaviour of the wasps was observed with a second video camera (RCA TC 2000, 25 mm/1.4 lens, camera 2), with time/date added to it (Panasonic WJ-810 time/date generator), on a monitor (Panasonic WV-5470). To make simultaneous observation of the behaviour of parasitoids and moths possible, we used a video splitter/inserter (RCA TC 1470) with which the image from camera 1 was projected in a window on the image from camera 2 on the monitor. Female moth calling activity was indicated by the extension of the terminal abdominal segments. Male moths responded to pheromone-loaded air with antennal movement, wing vibration and ambulatory activity. Further movement was limited by the enclosure of the glass container. A parasitoid was released into the olfactometer chamber only after calling activity of at least two of the female moths as well as a clear response of at least two of the male moths had been observed. For an observation to be classified as valid, the same had to apply to the checks made during and at the end of the 10-min observation. Other observations were discarded.

Experiment 2 was a control experiment to test whether the response of the parasitoids to the calling moths was indeed due to odours associated with calling activity and not to other cues ('general body odour'). We used the same method as in experiment 1, but here only the observations counted where no calling activity of any of the females, nor any response of the males was observed during any of the checks pertaining to an observation.

After every observation the olfactometer bottompiece and cover were thoroughly cleaned with hexane. The next observation was not started until the solvent traces had evaporated.

Recording of the parsitoids' behaviour was done with the aid of a TRS-80 Model 100 computer (Tandy Corp., Fort Worth, Texas, U.S.A.) programmed as an event recorder. Parameters measured for each observation were: the number of visits to the various odour fields; the proportion of time spent by the parasitoid in the four odour fields during the 10-min interval; whether or not an insect entered one of the arms; if so, whether or not it stayed there longer than 2 min ('final choice' *sensu* Vet *et al.*, 1983). All experiments were carried out at 26 ± 1 °C.

Results

Experiment 1. During the 10 min observations, the parasitoids made a significantly higher average number of visits to the flow field containing the odour of the moths than to the opposite control field. The adjacent control fields received intermediate numbers of visits (Table 1). Further, the insects stayed significantly longer in the flow field containing the odour of the calling moths, compared with the control fields (Table 2). Although 4 females entered the arm connected to the test field, none stayed there longer than 2 min.

Experiment 2. In the control experiment with non-calling virgin moths the total number of quadrants

Table 1. Average numbers of visits made by female *Trichogramma pretiosum* wasps to flow fields of the olfactometer.

Exp.	Odour source in test field	N	Flow field					P[1]
			Test	Left	Opposite	Right	Total[2]	
1	calling moths[3]	15	7.8	5.9	4.1	5.2	23.0	<0.01
2	non-calling moths	39	7.7	7.7	8.0	8.0	31.4	0.92

[1] Test of difference between numbers in test field vs. opposite field within one row (Mann-Whitney U test).

[2] Numbers in this column are significantly different (Mann-Whitney U Test, $P<0.01$).

[3] In 7 cases, only one moth was used, of which the behaviour was only monitored before and after the observations.

Table 2. Average percentage of time spent by female *Trichogramma pretiosum* wasps in flow fields of the olfactometer.

Exp.	Odour source in test field	N	Flow field				P[1]
			Test	Left	Opposite	Right	
1	calling moths[2]	15	58.3	14.2	13.5	14.0	<0.001
2	non-calling moths	39	20.1	26.7	21.7	30.5	<0.01

[1] Friedman two-way analysis of variance by ranks.

[2] In 7 cases, only one moth was used, of which the behaviour was only monitored before and after the observations.

visited was significantly larger than in experiment 1 and the visits were evenly distributed over the four flow fields (Table 1). Further, a preference for the odour of the moths was not exhibited. Instead, the parasitoids spent a significantly smaller proportion of their time in the test flow field compared with the adjacent control fields (Table 2). Also, only 5 out of the 39 females tested entered one of the arms, and no preference for any arm was shown.

Discussion

This study demonstrates that *T. pretiosum* can show a behavioural response to the odour emitted by calling *H. zea* moths. The odour led to a decrease in the total number of border crossings between fields and a higher number of visits to the odour permeated field compared with the opposite field. Further, the proportion of time spent in the calling moth odour field versus control air fields was significantly higher. The fact that a reaction of the wasps was elicited only be female moths during calling activity and concurrent with male moth responses, strongly suggests that the parasitoids were indeed responding to the sex pheromone of the moth. The reaction of *T. pretiosum* to its host's sex pheromone may be illustrative of a widespread phenomenon among egg parasitoids of Noctuidae, as similar effects have also been found for the palearctic species *T. evanescens*, parasitoid of *M. brassicae* (Noldus & van Lenteren, 1985a), as well as for *Telenomus remus*, parasitoid of *Spodoptera frugiperda* (Nordlund *et al.*, 1983).

These experiments confirm that the sex pheromone of *H. zea* serves as a kairomone for *T. pretiosum*. It seems adaptive indeed for an egg parasitoid to use host sex pheromone as an indicator for the probable presence of host eggs, because as far as known no other long distance cues more directly connected to the eggs themselves are available. However, our results do not provide much information about the mechanism causing higher parasitization rates in the field, as found by Lewis *et al.* (1982). A better understanding of the behavioural mechanisms governing the responses to these semiochemicals is essential for an interpretation of the present data in terms of searching efficiency and the eventual ability to manipulate such responses in the scope of biological pest control (Lewis & Nordlund, 1985; Jones, 1986). Attraction of parasitoids to infested areas has been proposed as an explanation (e.g., Wall, 1984; Vinson, 1986). However, in our olfactometer experiments the wasps were not *attracted* by the odour. As attraction should be reflected in a directed movement towards the odour source, we would expect that in our set-up wasps would walk into the test arms and make a final choice for the odour of the calling moths. However, the majority of the 10 min interval was spent in the exposure chamber. In experiment 1, only 4 wasps ever walked upwind into the test arm, but none stayed there longer than 2 min. Comparably, in the experiment of Noldus & van Lenteren (1985a), only 17 out of 44 insects walked upwind into the test arm, and only 7 made a final choice for the sex pheromone of *M. brassicae* (Noldus, unpubl.). This is in contrast to the attraction and high numbers of final choices often found with larval parasitoids in olfactometer experiments (Vet, 1985). These small numbers may be due to physical characteristics of the olfactometer set-up

(e.g., higher wind speeds around openings of arms, amount of light inside arms). Alternatively, *arrestment* by the host's sex pheromone rather than attraction may be the mechanism causing higher rates of parasitization in the field. Preliminary results of recent experiments in a windtunnel set-up indeed support this hypothesis (Noldus *et al.*, 1988a, b).

Other aspects of the odour of *H. zea* moths, in addition to the sex pheromone, apparently influence the searching behaviour of *T. pretiosum* as indicated by the repellent effect of the odour of non-calling virgin females in experiment 2. Noldus & van Lenteren (1985a) did not find significant repulsion by the odour of non-calling *M. brassicae* females (although the average proportion of time spent in this odour field was considerably shorter compared with control fields), but they did find smaller number of visits to the moth odour field (Noldus, unpubl.), which was not found in the present experiments. We do not yet have an interpretation for these effects.

One final aspect cannot be left unaddressed here. In the experiments described here, we have brought the parasitoids into direct contact with the odour of calling moths by rearing the latter under reversed photoperiod. However, in the field there is a gap in time between the release of sex pheromone by the host moths and searching activity of *Trichogramma* wasps. Calling activity by *H. zea* occurs during the night (Pope *et al.*, 1984; Raina *et al.*, 1986) and, although *Trichogramma* spp. will parasitize host eggs in darkness (Quednau, 1958; Klink, 1964), searching and parasitization activity in the field appears to be restricted to daytime (Ashley *et al.*, 1973). Evidence from the studies of C. Wall and colleagues (Wall *et al.*, 1981; Wall & Perry, 1983) suggests that adsorption of pheromone to vegetation might be the factor that makes this material available as a kairomone for diurnal parasitoids. Experiments are currently under way to test this hypothesis.

Résumé

Réponse du parasite oophage Trichogramma pretiosum *à la phéromone sexuelle de son hôte* Heliothis zea

Des expériences menées en olfactométrie avec le parasite oophage *Trichogramma pretiosum* Riley (Hymenoptera: Trichogrammatidae) et son hôte, *Heliothis zea* (Boddie) (Lepidoptera: Noctuidae) donnent les résultats suivants. La présence de la phéromone sexuelle de l'hôte réduit de façon significative le nombre de passages entre les champs odorisés. De mème, les parasites visitent plus fréquemment le champ qui dispense l'odeur de la femelle en appel que le champ témoin placé à l'opposé. Par ailleurs, le temps passé dans le champ qui contient la phéromone sexuelle émise par les femelles vierges en appel est siginificativement supérieur à la durée de visite des champs témoins. Si l'on utilise comme source d'odeur des femelles vierges qui ne sont pas en appel, la réponse est inversée, les parasites sont alors repoussés par l'odeur de ces papillons et le nombre de visites est distribué de façon aléatoire entre les quatre champs. Ces résultats sont discutés dans le contexte de l'écologie du comportement de recherche chez les parasites oophages.

Acknowledgements

Thanks are due to Lisa Hill for rearing the parasitoids, to Ray Sexton for help with construction of the set-up, to Oliver Zanen for use of the event recording program, to Piet Kostense for drawing the figure, to Laure Kaiser for translating the abstract, and to Joop van Lenteren, Jonathan Schmidt and Louise Vet for useful comments. The support by Joe Lewis during all stages of the research and preparation of the manuscript is gratefully acknowledged. This research was supported in part by cooperative agreement No. 58-319R-5-014 between the International Research Division of OICD-USDA and the University of Georgia. It is part of a cooperative program between the Insect Biology and Population Management Research Lab (USDA, Tifton, USA), the Insect Attractants, Basic Biology and Behaviour Research Lab (USDA, Gainesville, USA) and the Department of Entomology, Agricultural University (Wageningen, Netherlands).

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